

Non-neutral theory of biodiversity

GINESTRA BIANCONI¹, LUCA FERRETTI² AND SILVIO FRANZ³

¹ *The Abdus Salam International Center for Theoretical Physics, Strada Costiera 11, 34014 Trieste, Italy*

² *Facultat de Veterinaria and IFAE, Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain*³ *LPTMS, UMR 8626 CNRS et Université Paris-Sud, Bâtiment 100, 91405 Orsay CEDEX, France*

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Abstract. - We present a non-neutral stochastic model for the dynamics taking place in a meta-community ecosystems in presence of migration. The model provides a framework for describing the emergence of multiple ecological scenarios and behaves in two extreme limits either as the unified neutral theory of biodiversity or as the Bak-Sneppen model. Interestingly, the model shows a condensation phase transition where one species becomes the dominant one, the diversity in the ecosystems is strongly reduced and the ecosystem is non-stationary. This phase transition extend the principle of competitive exclusion to open ecosystems and might be relevant for the study of the impact of invasive species in native ecologies.

Understanding the basic principles responsible for the biodiversity in ecosystems is a fundamental questions of scientific and social interest. In fact many ecosystems recently, undergo a loss of biodiversity [1, 2] due to human activities or to non-native invasive species that in some cases might become dominant in the ecosystem.

Recently the *unified neutral theory of biodiversity and biogeography* [3] has been shown to reproduce species abundance distributions [4, 5] of meta-communities and local communities and the distribution of lifetimes [6] that are found in ecological systems. The proposed theoretical framework is based on the assumption that all species are equivalent and assumes that species abundance distribution is affected mainly by the drift resulting from a stochastic process of births, deaths and speciation. This theory raised some controversies in the field [7, 8], and there is an increasing need of a theory which includes the stochastic features of the neutral model but also accounts for the competitive advantage that some species might have in their niche. Moreover a non-neutral theory of meta-communities biodiversity has the potential to include also complex prey-predator foodweb relations [9–11] for which an increasing number of data is now available.

In the physics community non-neutral ecological models have been widely studied [11–13]. In this context a reference model is the Bak-Sneppen model [14, 15], which describes the extinction process in a non-neutral ecosystem. In the model, a negative selection process takes place

and at each step the less fit species of the ecosystem is removed, and mutations affect the species dependent on the removed one. This model leads to punctuated equilibrium and power-law extinction patterns found in fossil records.

In this paper we show that these two paradigms (the neutral model and the Bak-Sneppen model) can be recovered by a simple model of metacommunities ecological systems [11, 12] evolving following the principles of evolutionary dynamics, which include the fundamental ingredients of reproduction, negative selection and migration/speciation. In our stochastic model we assume that species are not equivalent but they are characterized by a quenched parameter that encodes for the adaptation of the species to their niche. We call this parameter the fitness of the species. High fitness will imply a competitive advantage of the species as in evolutionary models. In particular high fitness will increase the probability of reproduction of a species, and reduce the death probability due to a negative selection process. In the model speciations processes are included and we assume that they occur mainly as a consequence of migration events, in order to describe invasive species arriving at fixed rate in an ecosystem. This model reduces to the neutral theory of biodiversity in the limit in which all species have the same fitness. On the other side when we include the effect of evolutionary selection on species of heterogeneous fitness the model has a rich phenomenology. In the limit in which only negative selection is present, and considering

an extremal dynamics, we recover a dynamics that can be mapped into the mean-field Bak-Sneppen model [14, 15]. Moreover the model shows a phase transition to a non-stationary state in which one species becomes the dominant species in the ecosystem and the biodiversity of the ecosystem is strongly reduced. This phase transition is a condensation phase transition that in some limiting cases can be mapped to a Bose-Einstein condensation and is closely related to the condensation transitions found in different evolving models [16–20]. Below this phase transition, relevant dynamical effects take place and the condensed species with a finite population change in time in a nontrivial way.

Non-neutral birth-death dynamics of the ecosystem - We generalize the stochastic birth-death dynamics giving rise to the distribution of species in meta-communities in the neutral theory of biodiversity to a birth-death dynamics depending on quenched variables assigned to the species and that correspond to their niche adaptation. We call this quenched variable the fitness f of a species. We consider an ecosystem formed by N individuals belonging to S species with the number of individuals N fixed but a variable number of species S . Each individual belongs to a species $i = 1, 2, \dots, S$ and each species i has fitness $f_i > 0$. The birth-death dynamics is inspired by evolutionary dynamics and three different birth-death processes take place. We call this three processes replication, negative selection and migration/speciation. Starting from a random initial condition we define the following birth-death process:

- **Replication** - At rate α an individual of the species i with fitness f_i is chosen to replicate with probability $w(f_i)$, where $w(f)$ is an increasing function of the fitness, and is substituted by a random individual of the ecosystem. Therefore the resulting process is

$$n_i \rightarrow n_i + 1 \quad \text{and} \quad n_j \rightarrow n_j - 1 \quad (1)$$

and the species i and j are selected according to the probabilities Π_i^R and Π_j^R respectively, defined as

$$\Pi_i^R = \frac{w(f_i)n_i}{\sum_{\ell} w(f_{\ell})n_{\ell}} \quad \text{and} \quad \Pi_j^R = \frac{n_j}{N}. \quad (2)$$

This is the usual process of reproduction in population dynamics in which $w(f_i)$ describes the mean number of expected off-springs of the individual i .

- **Negative selection** - At rate γ an individual of a species i with fitness f_i is removed from the population with probability $B(f_i)$, which is a decreasing function of the fitness f_i and is substituted by an off-spring of a random individual. The resulting process is

$$n_i \rightarrow n_i - 1 \quad \text{and} \quad n_j \rightarrow n_j + 1 \quad (3)$$

and the species i and j are selected according to the probabilities Π_i^{NS} and Π_j^{NS} respectively, defined as

$$\Pi_i^{NS} = \frac{n_i B(f_i)}{\sum_{\ell} B(f_{\ell})n_{\ell}} \quad \text{and} \quad \Pi_j^{NS} = \frac{n_j}{N}. \quad (4)$$

This is a term of negative selection and describes the struggle for survival of the individuals. In particular $B(f_i)$ we take

$$B(f_i) = 1/w(f_i) \quad (5)$$

describing the Darwin concept of removal of the less fit species. More general form of $B(f)$ might instead represent barrier between fitness peaks in some complex fitness landscape.

This type of process is the pivotal process of the Bak-Sneppen model which is in addition also extremal (at each time-step the less fit species is removed from the ecosystem or migrates away from the metacommunity). We observe here that in our model when $\alpha = 0$, $\gamma < 1$ and $\beta \rightarrow \infty$, we recover an extremal dynamics that is reminiscent of the Bak-Sneppen model [14, 15].

One might naively think that the effect of the negative selection process and of the reproduction process is equivalent. This is not the case in general as it will be shown in the following.

- **Migration/Speciation** At rate $\mu = 1$ a migration/speciation occurs and a random individual is substituted with an individual of a new species $i = S + 1$. The new species is assigned a fitness f_{S+1} randomly drawn from a fixed distribution $\rho(f)$. The resulting process is

$$n_{S+1} \rightarrow 1 \quad \text{and} \quad n_j \rightarrow n_j - 1 \quad (6)$$

where the species j is selected with probability $\Pi_j^M = \frac{n_j}{N}$ and the fitness f_{S+1} is drawn from a distribution $\rho(f)$. We consider here on purpose only the case in which the new species have fitnesses independent on the fitnesses of the species present in the ecosystem. This is the case of speciations due to migration from another metacommunity which is relevant for the study of invasive species in given ecosystems.

In particular we consider the case in which the function

$$w(f_i) = e^{\beta f_i}. \quad (7)$$

where β is a tunable parameter. The assumption (7) is by no means a limitation since the model could be defined equivalently only in terms of the distribution of the variables $\{w\}$'s. Moreover the choice of the assumption (7) has the following advantages:

- i) It ensure that we have always $w(f_i) > 0$.

- ii) It allows to mimic the impact of the environment in driving the system out of neutrality, by changing β . In fact β tunes the relevance of the fitness in the stochastic dynamics. In particular when $\beta = 0$ we have $w_i = 1 \forall i$ and in the dynamical process all species are equivalent, recovering the neutral birth-death model.

Solution of the model - We study the master equation of the stochastic process describing the non-neutral dynamics taking place in the model ecosystem. If we call $N_n(f, t)$ the number of species of fitness f populated by n individuals, its master equation is given by

$$\frac{dN_n(f, t)}{dt} = b_{n-1}N_{n-1}(f, t) - b_nN_n(f, t) + d_{n+1}N_{n+1}(f, t) - d_nN_n(f, t) + N\rho(f)\delta_{n,1}, \quad (8)$$

where the birth rates b_n and death rates d_n are given by

$$\begin{aligned} b_n(f) &= \frac{n}{N}B(f) - \left(\frac{n}{N}\right)^2 C(f) \\ d_n(f) &= \frac{n}{N}D(f) - \left(\frac{n}{N}\right)^2 C(f) \end{aligned} \quad (9)$$

with $B(f) = \alpha e^{\beta f}/Z_1 + \gamma$, $D(f) = 1 + \alpha + \gamma e^{-\beta f}/Z_2$ and $C(f) = \alpha e^{\beta f}/Z_1 + \gamma e^{-\beta f}/Z_2$ and where we have defined Z_1, Z_2 as

$$\begin{aligned} Z_1(t) &= \frac{1}{N} \int df \sum_n e^{\beta f_i} n N_n(f, t) \\ Z_2(t) &= \frac{1}{N} \int df \sum_n e^{-\beta f_i} n N_n(f, t). \end{aligned} \quad (10)$$

In order to solve the master equation (8) we assume that $Z_1(t)$ and $Z_2(t)$ in the asymptotic limit $t \rightarrow \infty$ converge to a constant value

$$Z_{1/2}(t) \rightarrow Z_{1/2} + \mathcal{O}(N^{-1/2}) \quad (11)$$

In this assumption, the steady state of the master equation (8) can be solved exactly as in neutral birth-death models [4,5] giving the distribution of the abundance of the species with given fitness. The stationary solution for $N_n(f)$ is given by

$$N_n(f) = N \frac{\rho(f)}{d_1(f)} \prod_{i=2}^n \frac{b_{i-1}(f)}{d_i(f)} \quad (12)$$

In the limit in which $n \ll N$ this distribution becomes a convolution of different Fisher log series distribution [5]

$$N_n(f) = N \frac{\rho(f)}{D(f)} \frac{[\theta(f)]^{n-1}}{n} \quad (13)$$

with the diversity number $\theta = \theta(f)$ dependent on the fitness of the species f according to the relation

$$\theta(f) = B(f)/D(f) = \frac{\alpha e^{\beta f}/Z_1 + \gamma}{\gamma e^{-\beta f}/Z_2 + (\alpha + 1)}. \quad (14)$$

From now on we focus on this model in the case of bounded fitness distributions with $f \in [f_m, f_M]$ for which we might expect that, at least in a certain region of the phase space we might have a stationary state of this evolutionary dynamics. Without loss of generality we take from here on $f \in [0, 1]$. In this case the diversity parameter $\theta(f)$ reaches a maximum at the maximal fitness $f = 1$. The average number of individuals with a given fitness f is

$$\langle n(f) \rangle = N \frac{\rho(f)}{1 + \alpha - \gamma + \gamma e^{-\beta f}/Z_2 - \alpha e^{\beta f}/Z_1} \quad (15)$$

This distribution admits two relevant limits $\alpha = 0$ and $\gamma = 0$. To show this, it is useful to put $f = 1 - \varepsilon$ and to define a distribution $g(\varepsilon) = \rho(1 - \varepsilon)$. In absence of negative selection, i.e. $\gamma = 0$, the average number of individuals of fitness $f = 1 - \varepsilon$, $\langle n(f) \rangle$ can be expressed in terms of a Bose-Einstein distribution of the occupation of the energy level ε .

Conversely when reproduction selection are absent, i.e. $\alpha = 0$, the average number of species $\langle n(f) \rangle$ with fitness $f = 1 - \varepsilon$ follows a Fermi-Dirac occupation of the energy levels ε , provided that the negative selection processes occur at a smaller rate than speciation, i.e. when $\gamma < 1$. This show clearly that the distribution of species in this evolutionary dynamics change significantly if only the reproduction selection process occurs or if only to the negative selection process occurs. Moreover taking the limit $\beta \rightarrow \infty$ for $\alpha = 0$, $\gamma < 1$, we recover for $\langle n(f) \rangle$ the step function characteristic of the Bak-Sneppen model [14] and we can map the dynamics to the dynamics of a mean-field Bak-Sneppen model [15] showing punctuated equilibrium.

Eq. (13) and Eq. (15) are well defined once Z_1 and Z_2 are found self-consistently. The self-consistent equations read

$$\begin{aligned} Z_1 &= \int_0^1 d\varepsilon g(\varepsilon) \frac{e^{-\beta \varepsilon}}{1 + \alpha - \gamma + \gamma e^{\beta \varepsilon}/Z_2 - \alpha e^{-\beta \varepsilon}/Z_1} \\ Z_2 &= \int_0^1 d\varepsilon g(\varepsilon) \frac{e^{\beta \varepsilon}}{1 + \alpha - \gamma + \gamma e^{\beta \varepsilon}/Z_2 - \alpha e^{-\beta \varepsilon}/Z_1}. \end{aligned} \quad (16)$$

These self-consistent equations have to be solved for each given parameter value (α, γ, β) and each distribution of the fitness $\rho(f) = g(\varepsilon = 1 - f)$. Eqs. (16) might lack a solution when the maximal fitness value is reached in the system at infinite time, i.e. when $\lim_{f \rightarrow f_M} \rho(f) = \lim_{\varepsilon \rightarrow 0} g(\varepsilon) = 0$. In this case, an inverse critical temperature can be evaluated [21] such that for $\beta < \beta_c$ the Eqs. (16) have a solution while for $\beta > \beta_c$ they do not. This phase transition can be mapped in the case $\gamma = 0$ to a Bose-Einstein condensation phase transition in a Bose gas. As in the Bose-Einstein condensation the lowest energy state gets a finite occupation, in this model when $\beta < \beta_c$ we observe the emergence of dominant species in the ecosystem having a finite fraction of the total population. This dominant species can change with time and the ecological system is non-stationary. We observe here that

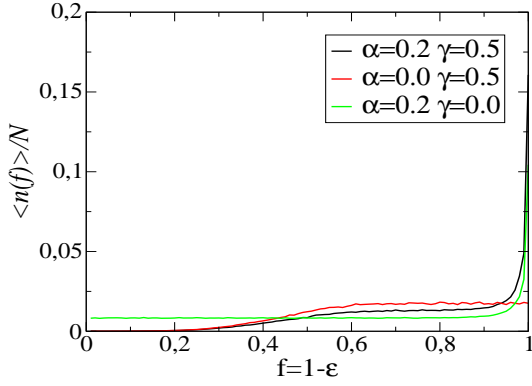


Fig. 1: Fraction of the individuals of the population with fitness $f = 1 - \varepsilon$ for a uniform distribution $\rho(f)$ with $f \in [0, 1]$. The data are shown for $\beta = 20$ and are averaged over 100 runs of the non-neutral birth-death dynamics involving a population of $N = 1000$ individuals. The data are collected at the time $T = 5 \times 10^4$ of the stochastic dynamics.

the time needed for an increase in the average fitness of the ecosystem in the condensed state increase with time in a multiplicative way. In fact we can say that this evolutionary model show in this limit relevant aging effects. This aging phenomena might be quite unrealistic for real ecologies. This feature of the model can be overcome by including genetic mutations that can occur on very long time scales. Genetic mutations are therefore negligible if we consider an ecosystem which reach quickly the steady states, but they can have relevant effects on the time scales of the aging dynamics of the ecosystem in the condensed phase.

Numerical characterization of the stationary and non-stationary state of the ecosystem - We have simulated the model and studied the population distribution and collected numerical evidence for the condensation phase transition to a non-stationary state. In fig. 1 we report the total population $\langle n(f) \rangle$ as a function of the fitness $f = 1 - \varepsilon$ for a uniform fitness distribution $\rho(f) = 1$ with $f \in (0, 1)$. The figure shows that at low temperature, in absence of the reproduction process, high fitness species are not rewarded by the non-neutral birth-death dynamics. On the other hand, in absence of the negative selection process, low fitness species are not punished by the non neutral birth-death dynamics. In order to study the non-stationary condensed state, we consider a fitness distributions of the type $\rho(f) = (\kappa + 1)(1 - f)^\kappa$.

In fig. 2 we report the time dependence of the fraction of individuals in the most populated species above and below the condensation transition. Above the condensation phase transition only an infinitesimal fraction of the total population belongs to the most abundant species, while below the condensation transition the dominant species is populated by a finite fraction of all individuals. The dominant species changes over long time scales as it is eventually overcome by other fitter species arriving later

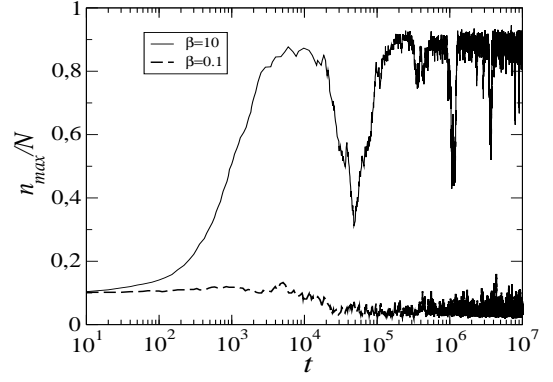


Fig. 2: Time dependence of the fraction of individuals in the dominating species below ($\beta = 10$) and above ($\beta = 0.1$) the condensation phase transition. Below the phase transition the non-stationary of the process is manifest with the most dominating species changing over long time scales. The data represent a single run of the evolutionary dynamics with parameters $N = 1000$, $\alpha = 10$ and $\gamma = 0.1$ and $\kappa = 0.1$. The critical value of the inverse temperature for these parameters is given by $\beta_c = 2.4$.

in the ecosystem. This process is the process that generalize the principle of competitive exclusion to open ecologies. In close ecologies the competitive exclusion principle in fact states that at long time scales, the fittest species of the ecosystem is fixated with higher probability. Here we prove that, in the presence of migration, the ecology might become dominated by a species with high fitness.

In order to characterize the phase transition as a function of β we studied the order parameter n_{max}/N indicating the fraction of individuals in the dominating species. Going across the condensation phase transition toward the non-stationary condensed state, the diversity of the population rapidly decreases as it is shown in Fig. 3 where we plot the total number of species S/N as a function of β . Moreover the inhomogeneity in the systems increases strongly below the condensation phase transition. In order to measure this inhomogeneity we plot the parameter δ defined as $\delta = -\frac{\ln(Y_2)}{\ln(S)}$ with Y_2 indicating the participation ratio of the species population, i.e. $Y_2 = \sum_{i=1}^S \left(\frac{n_i}{N}\right)^2$.

The participation Y_2 varies from $Y_2 = 1/S$ when all the species are equally populated to $Y_2 = 1$ when one species dominates the population. Therefore the parameter $\delta \in (0, 1)$ is equal to $\delta = 1$ for equally populated species and is $\delta = 0$ when only one species is occupied. In fig. 3 we show how n_{max}/N , S/N , and δ varies across the condensation transition as a function of β .

Conclusions - In this paper we have proposed a new, simple, non-neutral stochastic model for ecosystems in which species compete for finite resources. In the model we distinguish different limiting cases:

- Case $\beta = 0$ - We recover the *Neutral Model of the Unified Theory of Biodiversity* with species abundance distribution that can be approximated by a log Fisher

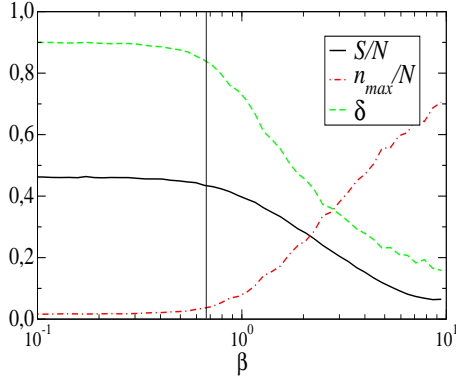


Fig. 3: The normalized number of species S/N , the fraction of individuals in the dominating species n_{max}/N and the parameter δ which measures the diversity in the population as a function of β across the phase transition for $\alpha = 1.5$, $\gamma = 1.5$ and $\kappa = 1.0$, $N = 1000$. The solid line indicates the value of the critical inverse temperature.

distribution with diversity parameter given by Eq. (14), therefore $\theta = (\alpha + \gamma)/(1 + \alpha + \gamma)$.

- Case $\beta > \beta_c$ - We have a stationary ecology where the species abundance can be approximated by a convolution of log Fisher distributions with diversity parameter dependent on the fitness $\theta = \theta(f)$ given by Eq. (14) and constants Z_1 and Z_2 satisfying Eq.(16).
- Case $\beta < \beta_c$ - We have a non stationary ecology with a dominating species and strongly reduced diversity. The phase transition at $\beta = \beta_c$ extends the principle of competitive exclusion to open ecosystems with high migration rate and shed light on the instabilities found in presence of high fitness invasive species.
- Case $\alpha = 0$ and $\beta \rightarrow \infty$ - We find a dynamics of extinctions that can be mapped to a mean-field Bak-Sneppen model and it can be shown [21] that this model shows punctuated equilibrium.

We believe that the proposed model can provide a general framework for the study of non-neutral models of biodiversity, presenting in a unified framework different known limits of stochastic dynamics of ecosystems. Work on progress is investigating extensions of this model for the description of ecosystems with non-trivial foodweb prey-predator or mutualistic interactions.

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